

Interactions between nitric oxide and plant hormones in aluminum tolerance

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Abbreviations: ABA, abscisic acid; Al, aluminum; AUX1 (auxin influx carrier), auxin resistant; CK, cytokinin; DTZ, distal transition zone; GA, gibberellic acid; IAA, indole-3-acetic acid; NO, nitric oxide; PIF, phytochrome interacting factor; PIN, pin-formed; RGA, GA receptor; TDZ, thidiazuron

Nitric oxide (NO) is involved, together with plant hormones, in the adaptation to Al stress in plants. However, the mechanism by which NO and plant hormones interplay to improve Al tolerance are still unclear. We have recently shown that patterns of plant hormones alteration differ between rye and wheat under Al stress. NO may enhance Al tolerance by regulating hormonal equilibrium in plants, as a regulator of plant hormones signaling. In this paper, some unsolved issues are discussed based on recent studies and the complex network of NO and plant hormones in inducing Al tolerance of plants are proposed.

Aluminum (Al) toxicity is a major limiting factor for crop production in acid soil, accounting for 30–50% of the world's arable lands. The root elongation growth in plants exposure to Al is rapidly inhibited. Plant species have evolved diverse mechanisms of Al tolerance including external exclusion and internal chelation.¹ However, most of the proposed mechanisms remain to be thoroughly deciphered. As a diffusive signal molecule, nitric oxide (NO) is also involved in Al tolerance in red kidney bean roots,² besides the reduction of endogenous NO underlies Al-induced inhibition of root elongation in *Hibiscus moscheutos*.³ We found that Al stress reduces endogenous NO levels in root apical cells and exogenous NO can ameliorate Al toxicity in plants.⁴ NO acts as a crossroad in hormone signaling to trigger metabolic and physiological responses.⁵ Since plant hormones can promote root elongation, research on interaction NO with plant hormones will facilitate to elucidate the role of NO improving Al tolerance.

Root apex is an important place where synthesizes plant hormones such as abscisic acid (ABA) and cytokinin (CK). Al treatment increased ABA content in the roots of maize, soybean, barley and pea, but not in sugar maple.⁶ ABA biosynthesis and signaling transduction are involved in aluminum tolerance of moss *Physcomitrella patens*.⁷ ABA may play an important role in regulating Al-resistance of soybean as an Al-stress signal.⁸ Al rapidly stimulated an increase of CK to inhibit root elongation

in *Phaseolus vulgaris*. The change in CK level precedes the Al-induced inhibition of root elongation, which may contribute to inhibition by promoting ethylene production or auxin accumulation.⁹ Al-induced ethylene production is associated with inhibition of root elongation in *Lotus japonicus*,¹⁰ but it is not a key factor in the Al-induced inhibition of root elongation that lags an increase of CK. Asymmetrical exposure of CK at the root tip promotes cell elongation, and ethylene signaling work downstream of CK of transducer the signal further. Moreover, auxin works downstream of both CK and ethylene, since differential auxin transport may cause differential cell elongation across the root by disrupting actin filament organization.¹¹ Al-induced ethylene evolution may serve as a signal to alter auxin distribution in roots by disrupting auxin influx carrier AUXIN RESISTANT (AUX1)- and PIN FORMED (PIN2)-mediated auxin transport, leading to arrest of root elongation.¹²

Auxin is an essential phytohormone in regulation of cell division and elongation.¹³ Al inhibits auxin transportation from shoot to root apices. Distal transition zone (DTZ) of the maize primary root plays an outstanding role in the Al response, a signaling pathway exists in the root apex to mediate the Al signal between DTZ and elongation zone through alterations in basipetal auxin transport.¹⁴ The alteration of IAA distribution leads to the arrest of root elongation under Al treatment. Synchronously, IAA might be involved in aluminum-induced efflux of malic acid from wheat by acting on anion channel.¹⁵ The regional patterning within the root cap is shifted by very short exposure to AlCl₃, which could be mimicked by application of the auxin-transport inhibitor.¹⁶ Auxin transport may be the target of Al toxicity, but polar auxin transport is insensitive to Al in Al-tolerant mutant *AlRes4* of tobacco.¹⁷ As disruption of polar auxin transport or signaling diminishes the effects of GA on root elongation, GA signaling during root elongation is known to require auxin. The attenuated growth response corresponds with reduced RGA (a specific DELLA protein) degradation in root cells. GA promotes growth by stimulating destruction of the nuclear growth-repressing DELLA proteins, which is a mechanism for environmentally responsive growth regulation.¹⁸

DELLA proteins are a common crosstalk node for several interacting hormones including auxin, ethylene and ABA.¹⁹ Auxin promotes the GA-induced destabilization of some of the

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DELLA proteins to affect GA responses.²⁰ Ethylene and ABA may also target DELLA proteins to exert antagonistic actions with GA during root growth. DELLAAs inhibit cell elongation by binding to the DNA-recognition domain of a transcription factor called PHYTOCHROME INTERACTING FACTOR4 (PIF4), as well as PIF3 and PIF5. This binding prevents the transcriptional activity of PIF from interacting with promoter elements and stimulating transcription of growth-related genes, but GA abrogates such repression by accumulating free PIF4 in the nucleus.²¹ Because ethylene, auxin and GA responses can be attributed to effects on DELLA function, DELLA plays a key integrative role in the phytohormone signal response network.²²

Taking NO as a mediator, we found that NO decreases the values of IAA/GA and IAA/ZR under Al stress. The value of ABA/(IAA+GA+ZR) is associated with the stress-resistance in plants. NO may improve Al tolerance by integrating the increase of ABA/GA, ABA/(IAA+GA+ZR) and the decrease of GA/ZR in plants.⁴ CKs and ethylene inhibit root elongation as consequence of endogenous IAA lowering and Cks enhancement. On the other hand, auxin and CKs strongly inhibits root growth through the promotion of ethylene production. But auxin recovers root meristem activity to promote root elongation by the establishment of an endogenous IAA/CKs ratio with higher IAA levels.²³ In addition, Cd-dependent reduction of NO level could alter Met adenosyltransferases (MAT-1) to increase ethylene biosynthesis.²⁴

Auxin, ethylene and NO can influence the production of the other two at different levels, which contribute to the amplification of an activation signal.²⁵ Transcripts putatively related to CK, auxin and ethylene metabolism were affected under Al treatment.²⁶ Because S-nitrosylation is a ubiquitous NO mediated posttranslational modification that might regulate broad spectrum of proteins, it may be another biological switch like phosphorylation.²⁷ Moreover, the ubiquitin-proteasome system plays a prominent regulatory role in plant hormone signaling pathway.²⁸ GA promotes proteasome-dependent degradation of DELLA in nuclei. A battery of signaling molecules are activated during Al stress and this flow of signals is not linear as considerable cross-talk takes place between signaling cascades.²⁹ Plant hormone signaling is integrated at several levels such as hormone distribution and gene expression during plant growth and development.³⁰

Different from animal, NO responds to stress through interaction with hormones in plants (Fig. 1). NO synthesis is not only induced by CK in tobacco, parsley and Arabidopsis,³¹ but is also induced rapidly by ABA in pea, *Vicia faba* and Arabidopsis. NO is probably a potential regulator involved in CK action in regulating energy absorption, trapping and conversion.³² Al stress may disrupt NO homeostasis,³³ which increases GA content. As a target of NO signaling, PIN1 links NO and auxin signaling in maintaining the size and activity of root apical meristem.³⁴ NO is an important molecule operating downstream of auxin through a linear signaling pathway during root growth and development.³⁵ NO supplementation can maintain auxin equilibrium by reducing the activity of IAA oxidase. GAs negatively regulated NO production, which promotes DELLA protein accumulation.³⁶ Co-operating with NO for stress tolerance, ethylene may

be a part of the downstream signal molecular in NO action.³⁷ NO and TDZ could decrease ethylene output by inhibiting ACC synthase activity.³⁸

In conclusion, NO and plant hormones coincidentally occur and can be mutually controlled in response to Al stress. In Al tolerance induction, NO and plant hormones often show overlapping and synergistic functions. The interactions and balances between NO and plant hormones under Al stress form a complex signaling network, which determine the Al-tolerant capacity of plants.

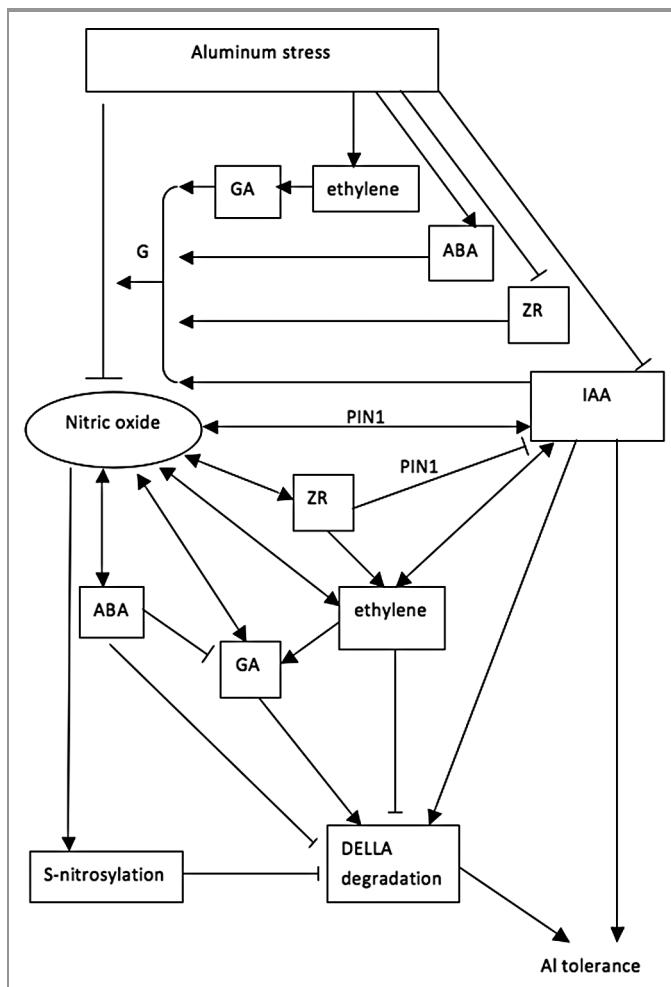


Figure 1. Schematic representation of the signaling network involving NO and plant hormones during plant responses to aluminum stress. Aluminum stress activates hormone signal transduction pathways and subsequently the G-protein transduces extracellular signals modulated by plant hormones such as IAA, GA, ABA and ZR. Al treatment reduces endogenous NO levels in plants. On one hand, NO induces the synthesis of plant hormones to regulate DELLA degradation, together with NO-mediated inhibition of ethylene biosynthesis. On the other hand, NO also promotes the degradation of DELLA protein through S-nitrosylation to improve Al tolerance. Furthermore, NO enhances PIN expression repressed by ZR to accelerate the transportation and synthesis of IAA, thereby reduce Al-inhibition of root elongation. G; G protein; (→) indicates synergism between signals; (↔) indicates activation of a physiological response; (→) indicates repressive response.

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